Time Course and Magnitude of Illusory Translation Perception During Off-Vertical Axis Rotation

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Vingerhoets, R.A.A., W. P. Medendorp, and J.A.M. Van Gisbergen. Time course and magnitude of illusory translation perception during off-vertical axis rotation. J Neurophysiol 95: 1571–1587, 2006. First published November 30, 2005; doi:10.1152/jn.00613.2005. Human spatial orientation relies on vision, somatosensory cues, and signals from the semicircular canals and the otoliths. The canals measure rotation, whereas the otoliths are linear accelerometers, sensitive to tilt and translation. To disambiguate the otolith signal, two main hypotheses have been proposed: frequency segregation and canal–otolith interaction. So far these models were based mainly on oculomotor behavior. In this study we investigated their applicability to human self-motion perception. Six subjects were rotated in yaw about an off-vertical axis (OVAR) at various speeds and tilt angles, in darkness. During the rotation, subjects indicated at regular intervals whether a briefly presented dot moved faster or slower than their perceived self-motion. Based on such responses, we determined the time course of the self-motion percept and characterized its steady state by a psychometric function. The psychophysical results were consistent with anecdotal reports. All subjects initially sensed rotation, but then gradually developed a percept of being translated along a cone. The rotation percept could be described by a decaying exponential with a time constant of about 20 s. Translation percept magnitude typically followed a delayed increasing exponential with delays up to 50 s and a time constant of about 15 s. The asymptotic magnitude of perceived translation increased with rotation speed and tilt angle, but never exceeded 14 cm/s. These results were most consistent with predictions of the canal–otolith-interaction model, but required parameter values that differed from the original proposal. We conclude that canal–otolith interaction is an important governing principle for self-motion perception that can be deployed flexibly, dependent on stimulus conditions.

INTRODUCTION

During passive motion in darkness, egomotion perception depends heavily on how the brain interprets signals mediated by somatosensory cues and by the two types of specialized vestibular receptors: the semicircular canals and the otoliths. The semicircular canals convey information about the angular acceleration of the head, whereas the otoliths sense gravitoinertial force (GIF), which is the vector sum of gravitational force and inertial force arising from linear acceleration. Thus the otoliths produce ambiguous information: they cannot distinguish between head translation and a change in head orientation with respect to gravity.

Many studies have tested human egomotion perception in the sole presence of canal cues (for review see Guedry 1974). A classical example is perception of egomotion in human subjects during constant-velocity yaw rotation about an Earth-vertical axis in darkness (Brown 1966; Young 1984). In this case, the motion percept starts out veridically, but then vanishes following an exponential decay, with a time constant of about 15–20 s. This decline is generally attributed to the high-pass filter characteristics of the canals in combination with a mechanism that extends the neural memory of head velocity, called velocity storage (Raphan and Cohen 1985; Raphan et al. 1979).

By contrast, both the canals and the otoliths are stimulated when subjects are rotated in yaw at a constant angular velocity, about a rotation axis that is tilted relative to the direction of gravity. In such motion conditions, referred to as off-vertical axis rotation (OVAR), the canals will initially sense the rotation, but their activity will again die out following an exponential decay. The otoliths, however, will be stimulated continuously by a rotating gravity component in the transverse head plane, which induces a sinusoidally varying linear acceleration along the interaural and nasooccipital axes. The frequency of these sinusoidal variations in shearing force is proportional to the rotation velocity, whereas their amplitude is proportional to the tilt angle.

A well-known example of an OVAR paradigm is “barbecue-spit rotation,” where subjects are rotated in yaw about an Earth-horizontal axis (i.e., OVAR with 90° tilt). When this occurs in darkness, subjects initially have a veridical rotation percept, but after some time they perceive an illusory translation along an orbital trajectory while facing a constant direction in space (Lackner and Graybiel 1978a,b; Mittelstaedt et al. 1989). The perceived direction of translational self-motion along the circular trajectory is opposite to the direction of the actual rotation. This illusion also occurs during rotation in roll or pitch at a constant velocity about an Earth-horizontal axis (see Bos and Bles 2002; Mayne 1974). Collectively, this type of illusion is often referred to as the Ferris wheel illusion because subjects experience a circular path of body motion without a sense of turning, just like in a gondola of a Ferris wheel.

Previous studies have also shown that, in darkness, subjects have an illusory percept of motion during OVAR even at small angles of tilt (Denise et al. 1988; for review see Guedry 1974). While subjects are actually rotated in yaw about a tilted axis (Fig. 1A), the perceived rotation velocity gradually decreases and a percept of head sway around a cone against the actual direction of movement emerges (Fig. 1, B and C). The decay of
rotation sensation is generally attributed to the high-pass characteristics of the canals, but the explanation of the illusory translation percept is still an unresolved problem. It has been suggested that the illusory translation percept during prolonged OVAR may reflect improper interpretation of the ambiguous otolith signal (Denise et al. 1988).

It is generally agreed that disambiguation of the otolith signal takes place at a central level in the nervous system. Two neural strategies for solving the problem have been proposed. First, the canal–otolith interaction hypothesis (see Fig. 2A) suggests that the brain uses an internal model, which combines information from canals and otoliths to differentiate translation from tilt (Angelaki et al. 1999; Bos and Bles 2002; Droulez and Darlot 1989; Glaser and Merfeld 1997; Merfeld 1995a;b; Merfeld and Zupan 2002; Merfeld et al. 1993; Zupan et al. 2002). In essence, this model exploits the canal signal to determine the changes in the otolith signal resulting from a reorientation of the head relative to gravity, and attributes the remaining part of the otolith signal to linear translation. Indeed, experiments on canal-plugged monkeys have suggested that semicircular canal signals are essential for the correct discrimination between different sources of linear acceleration needed to elicit appropriate oculomotor responses (Angelaki et al. 1999; Hass and Angelaki 1999).

The second hypothesis, known as the frequency-segregation model (see Fig. 2B), proposes that the ambiguity is resolved by filtering the otolith signal in two parallel pathways, such that high-frequency otolith signals are linked to translation, whereas low-frequency signals are ascribed to tilt (Mayne 1974; Paige and Seidman 1999; Paige and Tomko 1991; Seidman et al. 1998; Telford et al. 1997). The rationale behind this model is that gravity is a constant factor, effectively stimulating the otoliths in the low-frequency range. In contrast, translational movements are mostly short lasting, causing high-frequency changes in the otolith signal. Paige and Tomko (1991) provided support for this hypothesis on the basis of vestibuloocular reflex (VOR) responses in the squirrel monkey during sinusoidal head translation along the interaural axis. They found that torsional eye movements (reflecting tilt compensation) occurred mostly during low-frequency translation along the interaural axis, whereas horizontal eye movements (reflecting translation compensation) were elicited mainly during high-frequency interaural stimulation.

Although most efforts exploring the mechanisms of otolith disambiguation have concentrated on the oculomotor system (Angelaki et al. 2001; Haslwanter et al. 2000; Merfeld 1995a; Paige and Seidman 1999; Paige and Tomko 1991), the question arises whether the same principles apply to the perception of egomotion (Glasauer 1995; Merfeld et al. 2001; Mittelstaedt et al. 1989; Seidman et al. 1998). For example, the finding that subjects exposed to low-frequency linear acceleration on a sled have tilt percepts (Seidman et al. 1998) has been claimed as evidence for the frequency-segregation hypothesis. Merfeld et al. (2005b) recently reported different percepts for a given dynamic GIF stimulus, depending on whether it was imposed by tilt, translation, or a combination. These perceptual responses were best explained by the canal–otolith interaction model. By contrast, the oculomotor responses recorded in the same motion paradigm were much more consistent with the predictions of the frequency-segregation model. On this basis, Merfeld et al. (2005a,b) concluded that human oculomotor and perceptual responses depend on qualitatively different mechanisms.
Until now, the applicability of the two models to self-motion perception during OVAR has not been studied. The qualitative descriptions provided by previous studies (Denise et al. 1988; Guedry 1974) are insufficient to evaluate the two models in the perception domain. Our objective was to obtain quantitative measurements of self-motion percepts, both as a function of time and under conditions involving various degrees of otolith stimulation. For this purpose, we developed a novel method to assess psychophysical performance during OVAR at various tilt angles and velocities. Using these quantitative perceptual data, we tested whether the percept of translating along a cone (see Fig. 1B) has a time course and a pattern of stimulus dependency that would favor one of the two major hypotheses for otolith disambiguation.

**METHODS**

**Subjects**

Six males, ages between 24 and 60 yr (mean ± SD: 33 ± 14), gave written informed consent to participate in the experiments. Three of them (MK, NK, and SP) were totally naive regarding experimental goals. No systematic differences in performance were found between naive and nonnaive subjects. All subjects were free of any known vestibular or ocular disorders.

**Setup**

Subjects were seated comfortably in a computer-controlled vestibular chair that could rotate about any axis orientation in space. Chair position was measured with an angular resolution of 0.04°.

In the chair, subjects were secured with safety belts, hip and shoulder supports, and Velcro straps around the feet. The head was firmly fixed in a natural upright position for looking straight ahead using a padded adjustable helmet. The rotation axis of the chair was aligned with the middle of the interaural axis, parallel to the long body axis. The right eye was patched to avoid double vision.

A semitranslucent screen was attached to the chair at 0.27 m in front of the subject. A motor-controlled laser, fixed to the vestibular chair, rear-projected a red dot with an angular subtense of 2° on the screen. The velocity of this dot was computer controlled with an accuracy of 1°/s. The dot was used to determine the subjects’ perceived egomotion velocity in a psychophysical matching experiment (see Experiments).

**Experiments**

The experiments took place in complete darkness. Subjects were rotated clockwise (seen from above) about their yaw axis that was either vertical or tilted (15 or 30°) relative to the Earth-vertical (i.e., off-vertical axis rotation [OVAR]). Starting with the subject in left-ear down position, the constant velocity chosen for the experiment was reached within 3 s and then maintained for 3 min (see Fig. 3). Subjects were instructed to keep looking straight ahead during the experiments.

During the OVAR runs, all subjects reported that, initially, they felt themselves turning about their body axis. Later in the run, they perceived their head progressing counterclockwise along a conical path, at the frequency of rotation, while always facing the same direction in space (Fig. 1, B and C). All subjects felt the summit of the translation cone below the head. During each OVAR run, subjects indicated verbally when the cone illusion became first noticeable. In the case of vertical-axis rotation they signaled when their motion percept had disappeared. Furthermore, subjects gave an estimate of the radius, in centimeters, of the perceived circle described by their heads.

To quantify the self-motion percept, we used a two-alternative forced-choice task. During the run, at each nose-up (NU) and nose-down (ND) phase (see Fig. 3), the laser rear-projected a dot moving from left to right or from right to left for 350 ms, starting from the center of the translucent screen in front of the subject. In runs with vertical axis rotation, the laser dot was presented at the same points in time after rotation onset. Using a toggle switch, subjects indicated how the speed of the dot had to be adjusted (faster or slower) to be perceived as space fixed. Because the laser and the screen were head fixed, spatial stability was ensured only if the target moved away from the subject at the speed of perceived self-motion. An adaptive psychophysical procedure used the set of responses collected in a given run to update the speed of the dot to be presented at the same test points in the next run (see Psychophysical procedures). The purpose of this procedure was to adjust the movement of the laser dot on the head-fixed screen so that it appeared fixed in space. In effect, the velocity of the dot will then reflect the velocity of perceived self-motion and thus will be referred to as the subjects’ matching velocity.

As noted before, the subjects’ matching velocity could reflect a pure rotation percept, a pure translation percept, or a combination. Because rotational and translational velocities are expressed in deg/s and cm/s units, respectively, we present the matching velocity data in both units, using doubly labeled axes in the figures. In good approximation, the relationship between these units is given by

\[ v = \frac{\pi}{180} \cdot \alpha D \]

where \( v \) is the laser dot speed in meters per second, \( \alpha \) is the laser dot speed in degrees per second from the subjects’ perspective, and \( D \) is the screen distance in meters (Medendorp et al. 2002).

Subjects were tested in the NU and ND phases (see Fig. 3) in which the perceived lateral translation is near its maximum (see Fig. 1C). As a result, the interval between the stimuli, and thus the number of trials within a run, depended on the rotation speed. For example, at a chair velocity of 20°/s, a test trial occurred every 9 s. When using 50°/s, trials were performed every 3.6 s.

Between runs, there was a 90-s rest period during which the room lights were turned on to allow reorientation. In separate sessions, subjects were tested for different combinations of rotation velocity and tilt angle to be denoted as a speed series and a tilt series. The speed series consisted of the speeds 20, 30, 40, and 50°/s and was performed at a fixed tilt angle of 15°. Effectively, this means that the
otoliths were stimulated at frequencies of 0.056, 0.083, 0.11, and 0.14 Hz, respectively. The tilt series consisted of measurements at 0, 15, and 30° tilt at a fixed velocity of 30°/s. It took two to three sessions of about 40 min each to collect the data from the 18 to 20 runs constituting each experimental condition. Before measurements were taken, all subjects practiced a few runs to get used to the vestibular stimulation, the motion percept, and the task. The first experimental session of each subject was performed at a rotation speed of either 20 or 30°/s. In later sessions, the various conditions were tested in random order. Subjects never received feedback about their performance. All subjects performed the OVAR experiments at rotational velocities of 20 and 30°/s. As a result of OVAR-related nausea, one subject did not complete the 40°/s runs and two subjects did not participate in the 50°/s OVAR experiments.

Psychophysical procedures

During the first 110 s of the run (see Fig. 3), we used an adaptive-staircase procedure (for details see Ehrenstein and Ehrenstein 1999) to determine the velocity of the moving dot required for matching the subject’s perceived egomotion, at regular intervals after rotation onset. Matching velocity was defined as the dot velocity at which the response in repeated trials fluctuated between “faster” and “slower.” The idea behind the adaptive-staircase method is to present a series of ascending and descending dot speeds to find the stimulus level at which dot speed matches perceived egomotion. Because the percept of egomotion changed with time after rotation onset, it was necessary to perform this procedure for each and every trial within the entire sequence constituting the first 110 s of a run. Based on the collected series of responses (“faster” or “slower”) of a given run, the presentation in the forthcoming run was adjusted in the requested direction. Thus if the subject’s response to the first stimulus in trial n was “slower,” the next test stimulus would be presented at a slower speed, and so on, until the response to the same trial n in a later run reversed from “slower” to “faster.” Such a response reversal started a staircase-type series of adjustments in opposite direction until the next response reversal occurred. In this fashion, alternations between ascending and descending staircases straddled the matching velocity where “slower” and “faster” responses are equally probable. In line with common practice, the step size in the adaptive staircase, which began at a course level of 6 ± 1 deg/s in the first run, was reduced to a smaller value of 3 ± 1 deg/s later on, once the first two response reversals had occurred.

To illustrate how the adaptive-staircase procedure was applied in our experiments, Fig. 4A shows the stimuli presented in the first and second run of an OVAR experimental session. For example, in trial 4 of the first run, the stimulus moved at 15°/s and yielded a “slower” response. Accordingly, the test stimulus of trial 4 in the second run was adjusted to a lower level of 9°/s. Figure 4B shows how stimulus levels later in the session bounced up and down between two limits marked by multiple response reversals. Note reduction in step size after the second reversal, which occurred in the sixth run. With rare exceptions (<1%), the staircases from all subjects and all sessions yielded at least six reversals (typically eight to 12). The matching velocity was computed as the mean across the last six reversals.

Not noticeable for the subject, the final part of the run (110–183 s; see Fig. 3) served a different purpose. At this time, perceived self-motion had reached a steady state, which allowed us to obtain a further benchmark of vestibular psychophysics: the steepness of the psychometric function, which is a measure of noise in the egomotion signal (Green and Swets 1966). To collect these data, it was necessary to present a fixed set of stimuli, following a procedure known as the method of constant stimuli, which involves multiple presentations, in random order, of test stimuli in a predetermined range above and below threshold (see Ehrenstein and Ehrenstein 1999). This range was determined in earlier pilot experiments and consisted of at least 11 different velocities at intervals of 2°/s (equivalent to 0.94 cm/s). By presenting each laser dot velocity multiple times (typically 10), we determined the probability of getting a “slower” or “faster” response for each velocity. These scores were used to construct a psychometric function, under the assumption that the distribution of “faster” and “slower” responses is binomial, with a probability of getting a “slower” response given by P (see Eq. 1) and the probability of a “faster” response by 1 − P. Using the method of maximum likelihood (Wichmann and Hill 2001), we fitted a cumulative Gaussian curve to these data, given by

\[ P(x) = \Phi \left( \frac{x - \mu}{\sigma} \right) \]

where \( P(x) \) is the probability of a “slower” response, \( \Phi \) is the cumulative standard normal distribution, \( x \) is the stimulus level, \( \mu \) is the subject’s matching velocity, \( \sigma \) is the SD of the cumulative Gaussian, and \( \lambda \) is a parameter (0 < \( \lambda < 0.06 \)) that accounts for stimulus-independent errors (i.e., errors caused by subject lapses). This latter term refers to errors caused by subject lapses or mistakes, such as a misjudgment of the stimulus arising from a temporary lack of attention. These lapses are supposed to be task independent and can be excluded from the analysis by allowing \( \lambda \) > 0 (for details see Klein 2001; Wichmann and Hill 2001). The SD (\( \sigma \)) can be interpreted as a measure of the subject’s uncertainty about the perceived speed.

Data analysis

Data analysis was performed using programs written in Matlab (Matlab 6.0; The MathWorks). Unless otherwise specified, an ANOVA was used to determine whether differences in the results among various stimulus conditions were statistically significant (P < 0.05).

As will become clear in the RESULTS section, we fitted various types of analytical functions to describe the data in the most parsimonious fashion. We used the adjusted \( R^2 \) measure to evaluate and compare the goodness of fit. The adjusted \( R^2 \) is a correction on the normal \( R^2 \) statistic based on residual degrees of freedom. The notion of

\[ R^2 = 1 - \frac{SS_{res}}{SS_{total}} \]
“residual degrees of freedom” is defined as the number of response values minus the number of fitted coefficients. The adjusted $R^2$ is then given by

$$R^2_{adj} = 1 - \frac{\text{SSE}(n - 1)}{\text{SST} \cdot df}$$

in which SSE is the sum of squared residuals, SST is the sum of squares about the mean, $n$ is the number of responses, and df represents the residual degrees of freedom.

**Model simulations**

We used Matlab 6.0 and Simulink 4.0 (The MathWorks) to simulate the models outlined in Fig. 2. The predictions of these models will be discussed extensively in the DISCUSSION. Comparing the model predictions to the collected data of translation and rotation perception proceeded as follows. First, the model predictions of linear acceleration ($\ddot{a}$) and angular velocity ($\dot{\omega}$) were obtained as time-dependent three-dimensional (3D) vectors. The $z$-component of $\dot{\omega}$ was taken as the prediction of the model for the rotation component of our data. Because the illusory translation percept was quantified in the velocity domain, a transformation was needed to derive a velocity prediction from the acceleration output of the models. Therefore we separately integrated the components of $\ddot{a}$ and then computed the vector sum of the integrated $x$ (naso-occipital) and $y$ (interaural) components to obtain a model prediction for perceived translation velocity. In the DISCUSSION we will address the question of whether the integration process is perfect or leaky to some extent. The best-fit time constant of the leaky integrator was obtained by minimizing the sum of squared errors between models and data using the Matlab routine fmincon.

The canal–otolith interaction model was implemented following Merfeld and Zupan (2002). This model has four free parameters: $k_a$, $k_r$, $k_{tot}$, and $k_o$. In a first exploration of this model (Fig. 2A), we used the parameter values that Merfeld et al. (2005a) found suitable for egomotion perception: $k_a = -2$ rad/s per radian, $k_r = 1$ rad/s per radian, $k_{tot} = 1$, and $k_o = 3$. In further examination of this model, we searched within a limited parameter space to find out whether a different set of values would provide a better match to our data. Because of computational limitations the search was limited to the values $-0.5, -1, -2, -4, -$ and 8 for $k_a$, and 0.5, 1, 2, 4, and 8 for the other three parameters, yielding a total of 625 combinations.

We implemented the frequency segregation model following Telford et al. (1997) using a high-pass filter in the translation pathway and a low-pass filter in the tilt pathway (see Fig. 2B). Because we did not measure tilt perception in these experiments, the tilt pathway played no role in simulations with this model. To obtain predictions for the rotation perception we added an independent path that consisted of a first-order high-pass filter with a time constant of 23 s to approximate the combined effect of the canal dynamics and velocity storage cascade. This time constant yielded the smallest sum of squared errors for describing rotation perception. In the first series of simulations with this model, the high-pass filter in the translation pathway was modeled using a time constant of 0.05 s, as suggested by Telford et al. (1997), in combination with a perfect integrator. We also tested the predictions of this model in combination with a leaky integrator.

We used the root mean squared error (RMSE) as a measure for the goodness of fit to compare model predictions and data. The RMSE measure for the residuals is defined as the square root of the mean squared distance between the data points and the corresponding model prediction. Accordingly, RMSE values closer to 0 indicate a better fit. All model evaluations were based on the fit residuals from all conditions and subjects simultaneously. The set of parameters that yielded the minimal value for the sum of squared errors was defined as the best set.

**RESULTS**

We used two different approaches to investigate the effects of pitch tilt and rotation speed on the perception of egomotion induced by OVAR. Verbal reports were obtained about both the onset of the cone illusion and the radius of the perceived circular head trajectory in the steady state. The main body of results was collected using an adaptive psychophysical procedure that adjusted the speed of a briefly presented moving dot in the frontal plane such that it matched the speed of perceived egomotion.

**Verbal reports about the illusion**

At some point in the OVAR run, all subjects developed a percept of being translated along a cone. Figure 5 shows a histogram of the verbally reported onsets of this illusion, pooled across testing conditions. As shown, for each subject separately, the cone illusion started between 18 and 75 s (mean ± SD: 39 ± 14 s) after rotation onset, with considerable scatter in latencies within and across subjects. For example, subject JG reported the illusion noticeably later than subject SP (Fig. 5). There was no systematic effect of either tilt angle or rotation speed on the observed latencies [tilt angle: $F(3,20) = 0.15, P = 0.93$; speed: $F(2,17) = 0.2, P = 0.82$].

In the case of vertical-axis rotation, for which subjects reported when their sense of self-rotation had faded away, latencies ranged from 24 to 59 s (mean ± SD: 41 ± 12 s).

![Histograms of reported cone illusion latencies in seconds.](http://jn.physiology.org/)

**FIG. 5.** Histograms of reported cone illusion latencies in seconds. Responses pooled across experimental conditions. Most latencies were between 25 and 45 s with only a few cone onset times above 1 min. Subjects that completed all experimental conditions (JG, NK, RV, and SP) contributed about 100 estimates; the other 2, about 60.
These values were not significantly different from the illusion onset latencies obtained during the OVAR runs (t-test, \( P = 0.28 \)).

After each OVAR experiment, subjects provided an estimate of the radius of the perceived head trajectory during the cone illusion. Figure 6 shows the results for different rotation speeds and tilt angles. Across all subjects, the estimated radius ranged from 15 to 60 cm (mean ± SD: 32 ± 13 cm). A larger tilt angle increases the component of gravity stimulating the otoliths in the transverse head plane. This implies a larger acceleration component that could potentially be interpreted as translation, which in turn could lead to a larger perceived radius. However, the verbal estimates provide no support for this idea: the differences between the estimated radii for the 15 and 30° tilt conditions were not significant [\( F(1,11) = 0.83, P = 0.38 \)]. Likewise, there was no statistically significant effect of rotation speed on the estimated radii [\( F(3,20) = 0.48, P = 0.70 \)].

**Time course of self-motion percept**

To assess the time course of the self-motion percept at various tilt angles and rotation speeds, we used an adaptive-staircase procedure in the first 110 s of a run (see Figs. 3 and 4). With this procedure we determined egomotion-matching velocity as a function of time in the run. To introduce the description of these results, we start with the zero-tilt condition: rotation about an Earth-vertical axis at 30°/s. According to classical descriptions, the rotation sensations during Earth-vertical rotations in darkness decay to negligible values in a time interval of 20 to 40 s (Brown 1966; Guedy 1974; Young 1984). We found that the duration of the rotation sensation was approximately in this range, perhaps somewhat longer, as shown in the left panels of Fig. 7. These panels show the data from both test phases for all subjects (A) and the population average (D). In all subjects the matching velocity at the start of the run was near the actual value of 30°/s (Fig. 7A). As time proceeded, the matching velocity decreased exponentially, with the fastest decay reaching zero at about 30 s after rotation onset and the slowest about 60 s after rotation onset.

What is the time course of the motion percept when the rotation axis is tilted? As Fig. 7, B and C shows for all subjects separately, OVAR stimulation led to a different pattern of motion percepts in all subjects. In the initial part of the run, we observed no substantial differences: the matching velocity at the start of the run was perhaps somewhat larger than the actual value and then again followed an exponential decay. However, as can also be seen from the population averages (Fig. 7, E and F) clear differences between the NU phase and ND phase emerged after about 15 s. From this time onward, the self-motion percept bifurcated into two opposite velocity levels, instead of simply decaying to zero. These two opposite velocity levels reflect the subject’s perception of moving rightward in the NU phase as opposed to moving leftward in the ND phase, as schematically indicated in Fig. 1C. Noticeably, in the tilted-axis experiments there was more intersubject variability than in the Earth-vertical axis experiment. All curves bifurcated at about 15 to 45 s after rotation onset and then approached an asymptotic value, which we quantified by taking the mean of the last three data points from each curve. Table 1, which shows the asymptotic values of the matching velocities obtained in this fashion, suggests that the magnitude of the bifurcation increases with tilt angle. Indeed, a two-way ANOVA, with tilt angle (0, 15, and 30°) and rotation phase (NU/ND) as factors, revealed a significant two-way interaction [\( F(2,35) = 68.74, P < 0.0001 \)]. This confirms that the
TABLE 1. Asymptotic matching velocities

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<tr>
<th>Experimental Condition</th>
<th>Asymptotic Value, cm/s</th>
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<tr>
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<td>NU</td>
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<td>Tilt</td>
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<td>0°</td>
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Values are means ± SD.

The asymptotic values depend on both rotation phase and tilt angle.

These results are in agreement with anecdotal reports about self-motion provided after the experiments. Initially, subjects felt themselves rotating clockwise about their body axis. Later in the run, they felt themselves pivoting about a point some distance below the head, thus tracing a conical trajectory with their body, always facing the same direction in space. In combination, the rotation and the translation percept produced the matching velocity results shown in Fig. 7.

Figure 8 illustrates the matching velocities from all subjects separately (A–D) together with the population averages (E–H) in the speed series. In all conditions, after an initial exponential decay, the matching velocities for the NU and ND phases started bifurcating at some point between 15 and 45 s after rotation onset. Next, from 60 s after rotation onset onward, the matching velocities remained roughly constant in all subjects. Furthermore, it is evident from this figure that the magnitude of the bifurcation increased with rotation speed. The asymptotic values of the matching velocities are shown in Table 1. Again, the asymptotic values depended significantly on both rotation phase and rotation speed [F(3, 41) = 23.49, P < 0.0001].

Effect of tilt angle

Figure 9 presents the result of the decomposition analysis for all subjects in the tilt series. The top row depicts the putative rotation component, whereas the bottom row shows the reconstructed translation component. As the figure suggests, the decay of the R component showed a similar time course across tilt angles (see Fig. 9, A–C). For all tilt conditions, the rotation component showed an exponential decay to negligible values; thus no evidence for a persistent rotation percept was found. The translation component, however, clearly depended on tilt angle.

Decomposition of response curves

Anecdotal reports indicated that all subjects developed two distinct motion percepts in different phases of the experiment: an initial rotation percept, followed by a translation sensation. This suggests that there are contributions from two processes to egomotion perception during OVAR. In an attempt to separate these contributions, we decomposed the response curves to isolate the putative rotation component (R) and translation component (T). In this procedure, we assumed that R follows the matching velocity results shown in Fig. 7. At all rotation speeds the initial exponential decay bifurcates into 2 velocity levels after about 30 s. Bifurcation becomes more pronounced with higher speeds.

Figure 9 presents the result of the decomposition analysis for all subjects in the tilt series. The top row depicts the putative rotation component, whereas the bottom row shows the reconstructed translation component. As the figure suggests, the decay of the R component showed a similar time course across tilt angles (see Fig. 9, A–C). For all tilt conditions, the rotation component showed an exponential decay to negligible values; thus no evidence for a persistent rotation percept was found. The translation component, however, clearly depended on tilt angle.

FIG. 8. Time course of matching velocity during the speed series. A–D: matching velocities from all individual subjects. E–H: mean matching velocity computed from pooled results of all subjects. Speed series consisted of measurements at rotation speeds of 20, 30, 40, and 50°/s at 15° tilt. Format as in Fig. 7. B and F: same as B and E in Fig. 7. At all rotation speeds the initial exponential decay bifurcates into 2 velocity levels after about 30 s. Bifurcation becomes more pronounced with higher speeds.
angle. It equaled zero for the zero-tilt condition (Fig. 9D), in line with the fact that subjects did not perceive translational motion during this type of stimulation. For 15 and 30° tilts the translation component gradually climbed to an asymptotic level, in accordance with anecdotal reports. It is important to note that this increase did not always start immediately at rotation onset. In some subjects the increase was delayed by as much as 50 s. Another noteworthy observation is that there was more intersubject variability in the T components than in the R components at 15 and 30° tilts (compare Fig. 9, B and C to E and F).

We quantified the asymptotic level of the R component by again taking the mean of the last three points of the curve. Only the zero-tilt condition yielded a value (-1.22°/s, SD 1.04) that differed significantly from zero (t-test, P = 0.035).

**Effect of rotation speed**

Figure 10 shows the results of the decomposition analysis for the speed series. The top panels in Fig. 10, A–D illustrate that the R component followed a smooth stereotypic decay for all rotation speeds. As expected, there was a clear effect of rotation speed because as rotation speed increased the initial matching velocities increased correspondingly. In addition, just as in the tilt series, the rotation component decayed to an asymptotic level near zero, indicating the absence of a persistent rotation component. Again we quantified the asymptotic level of the R component by taking the mean of the last three points of the curve. Averaged across subjects, we found small positive values for each condition in the speed series, but these values were not significantly different from zero (t-test, P > 0.09 for each condition).
To quantify this temporal pattern, we fitted an exponential function to the data, expressed by

\[ R(t) = Ae^{-\frac{t}{\tau_R}} \]  

(3)

where \( A \) is the initial amplitude and \( \tau_R \) is the time constant of the decay. This is exemplified in Fig. 11A for the experimental condition with tilt angle 15° and rotation speed 30°/s, by showing the best-fit lines superimposed on the observed responses, for each subject. As shown, there is a close correspondence between the observed responses and the fitted curves. The fit parameters for all conditions are shown in Table 2. For all subjects and all conditions the fit results had goodness-of-fit values \( R^2 > 0.93 \). In all conditions, averaged across subjects, the fitted time constants (\( \tau_R \)) ranged from 12 to 32 s (mean ± SD: 20 ± 6 s). There was no significant effect of either tilt angle or rotation speed on the fitted time constants (\( \tau_R \)) \([F(5,32) = 0.58, P = 0.72]\). Table 2 also reveals that the fitted initial amplitude (\( A \)) was on average always larger than the imposed rotation speed. However, there was no significant effect of tilt angle on the fitted initial amplitude values \([F(2,15) = 1.67, P = 0.22]\). Not surprisingly, the effect of rotation speed on the initial amplitudes was significant \([F(3,20) = 13.9, P < 0.001]\). In summary, the R component decayed from an initial value somewhat larger than the imposed rotation speed and followed a stereotyped exponential decline that was independent of tilt angle and rotation speed. Potential factors that may have caused the initial overshoot, such as the proximity of the target and eye movements, will be evaluated in the DISCUSSION.

As in the tilt series (Fig. 9), the T component \((E-H)\) increased gradually with time. Again as in Fig. 9, the time course was less stereotyped than the decay of the rotation component, with more intersubject variability. Moreover, proper quantification of this response seemed to require inclusion of a pure time delay because in some subjects the rise of the T component could be delayed by as much as 50 s.

Quantitative analysis of R and T components

Taken together, Figs. 9 and 10 convey a strong suggestion that the rotation component follows an exponential decay to an asymptotic level near zero as the constant rotation continues. To quantify this temporal pattern, we fitted an exponential function to the data, expressed by

\[ T(t) = B\left[1 - e^{-\frac{t}{\tau_T}}\right] \quad \text{if } t < \Delta t \\ T(t) = B\left(1 - \exp\left[-\left(t - \Delta t - \tau_T\right)\right]\right) \quad \text{if } t \geq \Delta t \]  

(4)

where \( \Delta t \) is the delay, \( B \) is the asymptotic value, and \( \tau_T \) is the time constant of the exponential increase.

### Table 2.  
Best-fit parameters of decaying exponential fit to rotation component and of delayed exponential fit to translation component

<table>
<thead>
<tr>
<th>Experimental Condition</th>
<th>R Component</th>
<th>T Component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( A ), °/s</td>
<td>( \tau_R ), s</td>
</tr>
<tr>
<td>0° 30°/s</td>
<td>37.0 ± 4.0</td>
<td>18.7 ± 4.4</td>
</tr>
<tr>
<td>15° 30°/s</td>
<td>43.1 ± 12.7</td>
<td>23.9 ± 6.3</td>
</tr>
<tr>
<td>30° 30°/s</td>
<td>45.9 ± 7.0</td>
<td>19.5 ± 7.5</td>
</tr>
<tr>
<td>15° 20°/s</td>
<td>30.7 ± 3.7</td>
<td>20.9 ± 6.5</td>
</tr>
<tr>
<td>15° 30°/s</td>
<td>43.1 ± 12.7</td>
<td>23.9 ± 6.3</td>
</tr>
<tr>
<td>15° 40°/s</td>
<td>62.7 ± 14.7</td>
<td>19.7 ± 2.6</td>
</tr>
<tr>
<td>15° 50°/s</td>
<td>71.7 ± 19.7</td>
<td>19.7 ± 6.2</td>
</tr>
</tbody>
</table>

Values are means ± SD. Outliers (time constants >95 s) were excluded. The large SDs associated with the delay term are caused by large intersubject variability.

From a modeling perspective (see DISCUSSION), an important question is whether the decay in the rotation component and the rise in the translation component reflect a similar time course. To investigate this possibility, an exponential function should be fitted to the translation component as well. However, as described above, close scrutiny of the T component indicates that it did not always start immediately at t = 0. To account for this fact, we included a delay as an additional fit parameter to characterize the T component. If the decay in the R component and the rise in T component reflect a common time course, this delay should not differ significantly from zero. Thus we analyzed the T component using the following fit function

\[ T(t) = B(1 - e^{-\frac{t}{\tau_T}}) \quad \text{if } t > \Delta t \]  

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Table 2 displays the best-fit parameters and shows that the mean delays ($\Delta t$) ranged from 11 to 27 s across conditions. The individual delays ranged from 5 to 50 s (mean $\pm$ SD: $19 \pm 13$ s). The table also demonstrates that the asymptotic value ($B$) increased from about 5 cm/s at $20^\circ$/s to about 13 cm/s at $50^\circ$/s. For each condition, the averaged time constants ($\tau_R$) were generally close to 15 s. Pooled across subjects and conditions, they ranged from 5 to 40 s (mean $\pm$ SD: $15 \pm 9$ s). Figure 11B demonstrates the observed responses and their best-fit lines for the experimental condition with tilt angle $15^\circ$ and rotation speed $30^\circ$/s. For all subjects and all conditions, Eq. 4 described the data fairly well, $R^2 > 0.70$. Furthermore, we found positive values for the delay ($\Delta t$) for all conditions and subjects. This finding shows that the increase in the translation percept cannot be characterized by a simple exponential function with a single time constant, but that adding a delay, as in Eq. 4, is necessary for an adequate description of the data. This conclusion held if we corrected the goodness of fit for the number of parameters: the mean improvement in adjusted $R^2$ was 0.11 when the delay was included. Across individuals and conditions the increase in adjusted $R^2$ ranged from 0.005 to 0.284. An ANOVA revealed no effect of test condition on either the delay [$F(4,22) = 1.09$, $P = 0.38$] or on the fitted time constants [$F(4,20) = 0.08$, $P = 0.99$]. Consistent with our earlier observations, however, there was a significant effect of experimental condition on the asymptotic values of the T component [$F(4,20) = 7.6$, $P = 0.0007$].

For comparison, we tested whether a second-order linear model without delay, of the form $T(t) = B[1 - \exp(t/\tau_R)][1 - \exp(t/\tau_T)]$ could describe the T component equally well as the delay model specified by Eq. 4. The second-order model also gave a fairly good description of the data, with $R^2 > 0.70$. However, it was rarely better than the delay model. In the total set of 27 T components the second-order model was slightly better than the delay model in six cases, showing a mean improvement in $R^2$ of 0.009. In all other cases the delay model was better, with a mean increase in $R^2$ of 0.043. Thus overall, the combination of a pure time delay and a single exponential (Eq. 4) provided a better description of the T component. For the remainder of this report, we therefore adhere to this description of the data when discussing our results.

Relation between verbal reports and T and R components

To investigate whether the decay in R component and the rise in T component reflect a shared mechanism, as implied by the canal–otolith interaction model, we looked for correlations between the coefficients that quantify these components. A strong correlation was found only between the time constant of the rotation component, $\tau_R$, and the delay of the translation component, $\Delta t$ ($r = 0.73; P < 0.001; n = 27$). This means that translation percepts were more delayed when rotation percepts persisted longer, as would be expected when canal cues play a role in the onset of translation perception. A just significant correlation was found between $\tau_R$ and $\tau_T$ ($r = 0.40; P = 0.049; n = 25$), suggesting that, despite the additional delays associated with translation, canal and otolith signals may share some extent of neural processing.

Is there any relationship between the fitted parameters and the verbal reports? Linear regression analysis revealed that the verbally reported cone illusion latencies correlated moderately with fit parameters, $\tau_R$, $\tau_T$, and $\Delta t$, with correlation coefficients $>0.59$. This suggests, at least, that the verbal and psychophysical results are descriptions of the same phenomenon. Notably though, the reported verbal latency was typically longer than the fitted delay, with a mean difference of $19.7 \pm 11.2$ s across conditions and subjects. In other words, a detectable T signal had developed before subjects reported the cone illusion, indicating that the psychophysical method is more sensitive than the verbal reports.

Steady-state percept

The previous section described how the illusory motion percept develops over time during a constant-velocity rotation about a tilted axis. Figures 7–11 show that at about 90 s after rotation onset the percept of translational motion had stabilized in all subjects. To obtain a sensitivity measure for this steady-state translation percept, based on a psychometric curve, we used the method of constant stimuli in the final part (110–183 s) of the run (see Fig. 3 and METHODS). The psychometric curve, constructed on the basis of the responses, was characterized by three parameters: threshold; SD; and lapse rate, a correction for stimulus-independent errors (see Eq. 1). The threshold parameter can be regarded as the subject’s matching velocity, whereas the SD can be seen as a measure of noise in the signal. A small SD reflecting a steep curve implies that the subject is relatively certain about the perceived velocity.

To illustrate the results obtained with the method of constant stimuli, we first present the data from the zero-tilt condition. In this condition, subjects perceive themselves to be stationary, which should correspond to a threshold close to zero. Figure 12A

![FIG. 12. Psychometric curves obtained with the method of constant stimuli for the tilt series. Filled circles: ND measurements. Open circles: NU measurements. Solid line: fitted psychometric curve. Dotted line: 50% point, taken as the matching velocity. Curves for the NU phase and the ND phase are symmetrically spaced around zero. Matching velocities (in cm/s) increase with tilt angle. Subject JG.](http://jn.physiology.org/Downloadedfrom)
shows the psychometric curve fitted to the data from one subject in the 0° tilt experiment. Indeed, the thresholds for two test phases were very close to the expected value of 0 cm/s.

Figure 12, B and C shows that during OVAR at tilts of 15 and 30°, thresholds at NU and ND phases differed significantly and had opposite signs, consistent with the results from the first part of the run (staircase procedure, 0–110 s). Likewise, the magnitude of the matching velocity depended on tilt angle, with higher amplitudes for the 30° tilt angle. It also appears that the slope became less steep with increasing tilt angle, but this was not observed consistently in all subjects.

Earlier, we indicated that the net difference between NU and ND asymptotic values in the first 110 s of a run increased with rotation speed. The same trend was seen in the psychometric curves from the same subject as in Fig. 12. In all conditions, matching velocities were significantly different from zero and their amplitudes increased with increasing speed. Note also that the curves became less steep when rotation speed increased, which implies a decrease in the sensitivity for estimating the speed of self-motion. Table 3 shows the population means for the threshold and the SD in both the tilt series and the speed series. As shown, most trends observed in individual subjects in Figs. 12 and 13 also emerged in the pooled data. The threshold increased significantly with both tilt angle ($F(2,35) = 78.58$, $P < 0.0001$) and rotation speed ($F(3,41) = 26.44$, $P < 0.0001$). There was no significant effect of tilt angle (0, 15, 30°) or rotation phase (NU/ND) on the SD of the psychometric curves. By contrast, the SD of the psychometric curve increased with rotation speed ($F(3,41) = 5.68$, $P = 0.0029$), indicating that the sensitivity for self-motion decreased with increasing rotation speed.

Finally, we compared the matching velocities obtained with the method of constant stimuli to the asymptotic values found with the staircase procedure (see Time course of self-motion percept). A two-way ANOVA, with method (staircase or constant stimuli) and test condition as factors, revealed no significant main effects ($F(1,131) = 0.04$, $P = 0.851$, $F(5,131) = 0.07$, $P = 0.997$) or interactions ($F(5,131) = 0$, $P = 1.0$), indicating that both methods yielded consistent results.

**DISCUSSION**

Application of an adaptive psychophysical testing procedure allowed us to quantify time course and stimulus dependency of self-motion percepts during OVAR for the first time. The quantitative results were consistent with anecdotal reports from our subjects about their self-motion. All subjects sensed rotational motion during the initial part of the run, but then gradually developed an illusory percept of being translated in a direction opposite to the direction of rotation. We will first recapitulate our main experimental findings and compare them with previous reports. Then we will compare our results with predictions of the two contemporary models on otolith disambiguation, outlined in the introduction.

**Overview of main findings**

**VERBAL REPORTS.** The verbal reports from our subjects (Figs. 5 and 6) about the motion illusion are in quite good correspondence with earlier findings. The rotation percepts during vertical axis rotations lasted at least 24 and at most 59 s, somewhat longer than commonly reported in the literature (Brown 1966; Guedry 1974; Okada et al. 1999). A comparable range of values (18–75 s) was found for the onset of the translation percept during OVAR. Averaged across subjects and conditions we found a latency of 39 s. A similar latency was found by Guedry (1974), who reported values of about 45 s for 90° OVAR at 180°/s. Finally, the reported radii of the perceived cone during OVAR, ranging from 15 to 60 cm, are in the same
range as reported for the perceived cylindrical orbits during “barbecue-spit rotation” (Lackner and Graybiel 1978a). Taken together, our verbal reports provide confidence that the type of stimulation during our experiments has been effective in eliciting illusory motion percepts.

**Psychophysical Results.** To quantify the motion percept in more detail, psychophysical testing was performed at two phases during the rotation: the nose-up (NU) and nose-down (ND) phases. Using an adaptive-staircase method in the beginning of the run and the method of constant stimuli in its final part, we obtained matching velocities at regular intervals. The matching velocities were used as a measure of the subjects’ perceived egomotion. For the initial part of the run, the matching velocity reflected rotational motion, consistent with anecdotal reports. As time proceeded, the psychophysical results yielded two separate patterns for NU and ND that bifurcated into two different velocity levels, consistent with how subjects described the translation percepts that occurred later in the run.

More specifically, the translation was perceived as motion along an orbital path (leftward in the ND phase, rightward in the NU phase), without a sensation of turning. Which neural processes could have mediated the observed motion percepts?

As explained in the Introduction, OVAR stimulates both the semicircular canals and the otoliths. The semicircular canals gradually adapt, just as during vertical-axis yaw rotation, but the otoliths are modulated constantly because of the continuous reorientation of the head with respect to gravity. Do the time courses that we have observed reflect these processes? In an attempt to separate the putative contributions from the otoliths and the canals, we decomposed the responses from the NU and ND phases in terms of a rotation and a translation component. Basically, we followed an approach proven sound by others for separating the angular and translation VOR in postrotational tilt experiments (Merfeld et al. 1999; Zupan et al. 2000). Accordingly, subtraction of responses from both phases eliminated the rotation component and isolated the translation component. The mean of the two responses yielded the rotation component by removing the translation component.

**R component.** We found that the R component declined exponentially to zero in about 30 to 60 s after rotation began, which is again slightly longer than reported in previous studies (Brown 1966; Okada et al. 1999). It is also noteworthy that the R component always decayed to zero, without a convincing sign of the residual rotation percept reported anecdotally by Denise et al. (1988). Because this R pattern was found irrespective of tilt angle or rotation speed, it seems reasonable to conclude that the R component stems mainly, if not exclusively, from the semicircular canals.

How can it be understood that the rotation percepts in our study lasted longer than earlier reported? It is known that vision is dominant in motion perception, so that when a subject is rotated in a rich lighted environment the rotation percept will not decay, despite adaptation of the canals. In our experiments, subjects were exposed to a small visual stimulus that moved away from them as if it were a world-fixed point. This stimulus was presented twice in a cycle and may have prolonged the rotation percept.

We further found that the initial amplitude of the R component (see Table 2) was somewhat larger than the imposed rotation speed. What may have caused this phenomenon? One potential factor is eye movements. To determine the speed of the dot relative to the head, the brain needs to combine retinal motion and eye velocity. If eye velocity is only partly taken into account in this process, as suggested in the literature (Freeman 2001; Turano and Massof 2001; Wertheim 1994), this could explain why we found an overestimate of the initial speed. The spatial geometry of our setup, in which stimuli were presented close to the subject and the eyes were off-centric from the rotation axis, may also have contributed to the effect.

That is, rotations of the head cause the eyes to translate, so that a near target should move with a slightly greater angular velocity than that of the head to be perceived stationary in space. The relation between ideal gain (G), ocular eccentricity from the rotation axis (r), and fixation distance (D) can be approximated by $G = 1 + r/D$ (Medendorp et al. 2000; Telford et al. 1998). Applied to our situation, where $r$ is about 8 cm and $D$ is 27 cm, this predicts a gain of 1.3, which would largely explain the observed effects.

**T component.** Which sensory signals are reflected in the time course of the T component? As our results show, the envelope for the oscillatory translation perception gradually rose from zero levels to an asymptotic value, in both the speed and tilt series. During vertical axis rotations (i.e., tilt angle zero), all T curves straddled the zero line, in accordance with the fact that subjects never perceived translation during Earth-vertical axis rotation (see Fig. 9D). These results suggest that the steady-state T component reflects the otolith contribution to self-motion perception, consistent with the present findings that the T component increased at larger tilt angles that involve stronger forces stimulating the utricles. The magnitude of perceived translation velocity during prolonged OVAR can be transformed into a corresponding radius of the perceived orbit, based on the fact that the angular velocity in circular motion equals linear velocity divided by the radius. Using this relation, the expected perceived radius can be calculated by dividing the matching velocity by the angular velocity of the vestibular chair in radians. Such computations show that the observed translational velocities (5–13 cm/s; see Tables 2 and 3) correspond to perceptual radii of 6 to 23 cm, slightly smaller than the verbal reports (Fig. 6). In this context, it should be noticed that the verbal radii were independent of tilt angle, but the translation velocity values clearly were not. This discrepancy may reflect a difference in sensitivity between the quantitative psychophysical method and the reports based on introspection.

Finally, in all subjects, we found that the T component did not start immediately after rotation onset but could be delayed by as much as 50 s. We fitted a delayed exponential (Eq. 4) to capture this characteristic. Indeed, analysis showed that incorporating a delay significantly improved the fit. Another interesting finding in our experiments was that signs of an emerging translation signal could be detected well before a conscious awareness of head translation developed. This indicates that the translation signal may already have an effect at one level in the system (in this case, the detection of object motion) at a time when it has not yet penetrated the conscious percept of body motion in space.

**Perception versus action**

Many studies have been concerned with the eye movements elicited during OVAR in humans (Darlot et al. 1988; Furman
et al. 1992; Haslwanter et al. 2000; Wood 2002) and in monkeys (Angelaki and Hess 1996a,b; Kushiro et al. 2002). Although these studies have used various techniques and paradigms, their results are generally fairly consistent.

To see how the perceptual findings in our study relate to the oculomotor results, let us first compare our perceptual $\tau_R$ values to the time constants found by Haslwanter et al. (2000). In the case of Earth-vertical axis rotation they reported a time constant of about 17 s, close to the present value of 19 s. Haslwanter et al. (2000) further found that increasing the tilt angle shortens the time constant, but we did not see this reduction. Furthermore, human oculomotor studies have reported a significant positive offset in horizontal eye velocity in the steady-state situation after prolonged OVAR that increased with increasing tilt angle. Such positive offsets could reflect a persisting rotation percept, although the verbal reports and our psychophysical data provided no sign of such an effect.

Various oculomotor studies have reported a modulation in horizontal eye position that may represent a compensation for illusory head translation during OVAR (Angelaki and Hess 1996a; Darlot et al. 1988; Haslwanter et al. 2000). For example, Darlot et al. (1988) found horizontal eye position modulations of about 4°. Under the assumption that the eyes were at the dark vergence position, say at about 0.8 m in depth (Fisher et al. 1988), this 4° modulation would reflect a 6-cm cone radius, slightly smaller than the radii reconstructed from the matching velocities in this study. Wood (2002) rotated subjects about a 30° off-vertical yaw axis at various constant velocities. His results show a decrease in tilt-related and an increase in translation-compensatory eye movements as rotation speed increased. These findings are in line with the present results, showing that the magnitude of translation increased with rotation speed.

**Modeling aspects**

**WHY DID SUBJECTS EXPERIENCE TRANSLATION ALONG A CONE?** To better understand the translation illusion, it is helpful to consider the signals that would occur during actual motion along a cone. It can be shown that the type of conical motion perceived by our subjects would evoke the same pattern of otolith stimulation as evoked by OVAR. To illustrate this, we compared the motion signals during OVAR at 15° tilt and 30°/s (Fig. 14, A, C, and E) with those expected when actually moving along a cone with a 25-cm radius and a height of 1 m (Fig. 14, B, D, and F). Interestingly, to obtain the same otolith signals, with the interaural GIF component leading the nasooccipital component by 90°, the translation along a cone must proceed in a direction opposite to the OVAR rotation. Thus because of the ambiguity of the otoliths, the two conditions can be distinguished only if additional motion signals are available. Therefore a comparison of the rotation signals in the two situations is crucial. Figure 14, C and D shows that the rotations in the two simulated motion paradigms are very different. During OVAR, the subject is rotated only in yaw (Fig. 14C). During the cone motion, the yaw component is lacking but there is alternating right–left and front–back tilt (Fig. 14D). Finally, Fig. 14, E and F shows the expected canal signals. The point to be taken is that the canals will adapt during OVAR but not during actual cone motion at the simulated rotation speed. Thus these simulations illustrate the dilemma facing the brain when it has to interpret the otolith signal when the yaw rotation signal is weakening. The original interpretation of rotation about a tilted axis is no longer tenable. The alternative, motion along a cone, although perfectly compatible with the otolith signals, is not straightforward either because the vertical canal signals expected in that situation are lacking. Thus the brain is faced with a sensory conflict because, as the canals have decayed out, the sensory signals are compatible with neither the actual motion nor the illusion.

In this vein, an interesting analogy can be seen in results from centrifuge experiments. For rotations with a fixed radius, subjects developed a tilt percept that considerably lagged...
behind the temporal change in GIF caused by the centrifugal force (Merfeld et al. 2001). In this situation, the canals and otoliths initially provide accurate information and the motion percept is veridical. As the canals gradually adapt a tilt percept appears, as if the brain reluctantly interprets the GIF as arising from tilt although the subject is in fact upright. Our experiments, which provide the first quantitative assessment of illusory translation percepts during OVAR, also show that the central interpretation of the GIF signal, when canal cues are weakening, lags considerably behind, even with signs of a delay. Thus the situation here has a striking similarity with the fixed-radius centrifuge experiment, except that now subjects develop an illusory translation percept. Again, we see that it takes considerable time before the brain reluctantly adopts a new interpretation of the time-varying GIF signal.

As can be seen in Fig. 14F, during real cone motion vertical canal cues are present, but this is not the case during OVAR (Fig. 14F). Nevertheless our subjects did have tilt sensations: i.e., they felt conical rather than cylindrical movement. Thus these tilt sensations may reflect the interpretation of the ambiguous GIF signal, which is assigned partially to translation and partially to tilt. The central interpretation of the GIF signal is the theme of the canal–otolith-interaction model and the frequency-segregation model and will be discussed in the next paragraphs.

NEURAL STRATEGIES FOR OTOLITH DISAMBIGUATION. Denise et al. (1988) proposed a conceptual scheme to explain the illusory motion percepts during OVAR. According to their hypothesis, part of the GIF acting on the otoliths, actually caused by tilt, is incorrectly assigned to translation by the CNS. Various possible decompositions of the GIF into tilt and translation were considered, although no specific model allowing quantitative predictions was specified. More recently, new quantitative models have been developed, such as the canal–otolith interaction model (Angelaki et al. 1999; Bos and Bles 2002; Glasauer and Merfeld 1997; Merfeld and Zupan 2002; Zupan et al. 2002) and the frequency-segregation model (Mayne 1974; Paige and Seidman 1999; Paige and Tomiko 1991; Seidman et al. 1998; Telford et al. 1997), which make specific predictions about the disambiguation of the otolith signal. The final section of this paper will compare these predictions to our data. However, as Fig. 2 illustrates, making this comparison requires extension of these schemes because both models predict perceived translation acceleration, whereas we measured translation velocity. Thus for comparison with our velocity data, assumptions have to be made on how the brain integrates acceleration to yield velocity.

Canal–otolith interaction. As explained in METHODS, we obtained predictions from the canal–otolith interaction model by simulating the model proposed by Merfeld et al. (2005a) for our stimulus conditions. As a first step we used the parameters as specified by Merfeld et al. (2005a) and further assumed the integration from acceleration to velocity (see integration stage in Fig. 2A) to be perfect, compatible with behavioral evidence that the nervous system can accurately perform this integration (Israel et al. 1993, 1997; Medendorp et al. 2003). We will refer to this first model version as model C1. To quantify how well model C1 predicts the data, we present the RMSE (see METHODS) for each subject in Table 4. The RMSE measure was based on the joint fit to T and R components, and was expressed in deg/s. As shown in the first row, the RMSE values for model C1 reveal a poor fit: there is a huge discrepancy between the model predictions and the data. This discrepancy mainly reflects the overestimation of translation velocities. Model C1 predicts translation velocities ranging from about 200 to 325 cm/s, whereas we found much smaller velocities ranging from 5 to 14 cm/s. It is interesting to note that simply changing the gain of the output, after the internal model and the perfect integrator, would yield a negative correlation between steady-state translation velocity and rotation speed, whereas we found the opposite result. An alternative explanation for the magnitude difference that can also account for the relation between translation velocity and rotation speed is that subjects were not able to achieve perfect integration, as also suggested by Merfeld and Zupan (2002).

To explore this, we simulated the same canal–otolith interaction model (fixed parameters), combined with a leaky integrator (model C2). We found that model C2, in combination with a leaky integrator having a time constant of 0.04 s, provided the best prediction of the asymptotic translation velocities. This value of the time constant is somewhat smaller than the 0.1 s suggested by Merfeld and Zupan (2002). As Table 4 demonstrates, model C2 was much better than model C1 by showing much smaller RMSE values. Figure 15 shows the predictions of model C2 for perceived angular yaw velocity (Fig. 15A) and translation velocity (Fig. 15B) at 20°/s and 15° tilt. As can be seen, the time course of the R component roughly follows the prediction of the model, but the predicted initial amplitude is clearly smaller and the decay is a little too fast. Another prediction of model C2 is that the R component reverses sign at a late stage, which was however not observed in the present study. With respect to translation perception (Fig. 15B), model C2 predicts an exponential increase of the envelope of the oscillatory T component, which seems to fit with the observations. On average, the magnitude of the T component is well predicted by model C2. Thus it is clear that model C2 provides a better description of the data than model C1, as proposed by Merfeld et al. (2005a), combined with perfect integration. C2 is like C1 but combined with leaky integration. C3 is like C2 but with best-match parameters in internal model (see Fig. 2A). Parameter values for C2 and C3 were determined using pooled data from all conditions and all subjects. Dimensions: $k_r$, rad/s per radian; $k_{rot}$, rad/s per radian; $\tau_{\text{leaky}}$, s; RMSE, deg/s. Parameters $k_r$ and $k_{rot}$ are dimensionless.

<table>
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<th>Model</th>
<th>$k_r$</th>
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<td>1</td>
<td>3</td>
<td>63</td>
<td>349</td>
</tr>
<tr>
<td>C2</td>
<td>-2</td>
<td>1</td>
<td>3</td>
<td>0.04</td>
<td>8.6</td>
</tr>
<tr>
<td>C3</td>
<td>-4</td>
<td>2</td>
<td>8</td>
<td>0.04</td>
<td>5.7</td>
</tr>
</tbody>
</table>

TABLE 4. Performance of different versions of the canal–otolith-interaction model.
A internal model as explained in the METHODS section. The best-and searched for the optimal values of the parameters in the

Now that the magnitude problem was solved, we kept the time account for the delay seen in the data of most of our subjects. C1. It is important to point out that neither C1 nor C2 can

predicts an immediate onset of translation perception.

Frequency segregation model of the T component in the data and the model predictions is even larger than components of all subjects (thin lines). Discrepancy between the time course from Telford et al. (1997) and leaky integration (F2) superimposed on the T translation velocity from the frequency-segregation model with high-pass filter solid line), superimposed on the T component of all 6 subjects (thin lines). Prediction for angular velocity shows an

exponential decay to near zero values, just as in the data. Model C3 performs better than model C2. B: predicted translation velocity from the canal–otolith interaction model with original (C2, dashed line) and adjusted parameters (C3, solid line), superimposed on the T component of all 6 subjects (thin lines). Predicted time course rises faster than the data. C: predicted perceived angular velocity from the frequency-segregation model (F2). Canals and the velocity storage system are modeled by a high-pass filter with a time constant of 23 s. Prediction for angular velocity matches the data quite well. D: predicted translation velocity from the frequency-segregation model with high-pass filter from Telford et al. (1997) and leaky integration (F2) superimposed on the T components of all subjects (thin lines). Discrepancy between the time course of the T component in the data and the model predictions is even larger than that for the canal–otolith-interaction model. Frequency segregation model predicts an immediate onset of translation perception.

C1. It is important to point out that neither C1 nor C2 can account for the delay seen in the data of most of our subjects.

Finally, we tested a third version of the canal–otolith-interaction model (model C3), in which we searched for parameters that would improve the time course predictions. Now that the magnitude problem was solved, we kept the time constant of the leaky integrator fixed at 0.04 s (as in model C2) and searched for the optimal values of the parameters in the internal model as explained in the METHODS section. The best-match values were $k_a = -4$, $k_f = 2$, $k_{fa} = 8$, and $k_{iu} = 8$ (Fig. 2A). As shown in Table 4, model C3 yields the smallest RMSE values. Figure 15, A and B illustrates the predictions of model C3. The prediction of the R component has improved, i.e., model C3 predicts a slower time course than model C2. Model C3 also predicts a slower time course for the T component, providing a closer match to the data. However, like models C1 and C2, model C3 also failed to predict the delay observed in most subjects.

To explain differences in model performance we used a single condition for illustrative purposes, but our experiments were composed of several speeds and tilt angles. The data showed an increase of steady-state matching velocity with rotation speed from 5.1 to 12.6 cm/s (see Table 2). Model C3 predicted a smaller increase from 4.4 to 7.1 cm/s for the speed series. With respect to the tilt series, model C3 predicts an increase with tilt angle (5.8 to 9.7 cm/s), capturing the main trend seen in the data.

Frequency segregation. The model structure of the frequency-segregation model is depicted in Fig. 2B. We simulated various versions of this model, as outlined below. In model F1 we assumed perfect integration of linear acceleration to velocity. Incorporating perfect integration caused overestimation of the translation percept, but to a lesser extent than that in model C1. This is indicated by the RMSE values in Table 5. In model F2 we incorporated a leaky integrator in the translation pathway. Basically, model F2 reflects a similar proposal by Telford et al. (1997) for the translation VOR. The best-fit time constant of 0.68 s for the leaky integrator in model F2 was slightly larger than the value of 0.25 s suggested by Telford et al. (1997). Model F2 was a substantial improvement over model F1, as shown by its smaller RMSE values. Yet, the time course of the predicted T component, shown in Fig. 15D, was much faster than that in the data, reaching its final value within a few seconds.

To investigate how closely the model could match the observed data, we simulated model F3. Here, we searched for the best-match time constants of the leaky integrator and the high-pass filter. Nonetheless, we were unable to find a combination of time constants that could produce a time to peak beyond about 6 s, whereas our data require a time to peak of roughly 30 s. This result can be understood in terms of systems theory, from the characteristics of a high-pass filter. Recall that the constant-velocity stimulus during OVAR effectively stimulates the otoliths in a sinusoidal manner (Fig. 14A). Therefore an increase of this velocity would increase the frequency of the otolith input, without changing its amplitude. The time constant of the high-pass filter determines the extent of filtering at a given frequency. Thus the time constant effectively regulates the range of rotation velocities that will result in a significant translation perception. However, this can never explain the long time constants and delays associated with the translation perception. Clearly, the slow time course must be strongly related to the decay of the canal signal. For this reason, model F3 did not provide a better fit than model F2 and was not incorporated in Table 5 and Fig. 15. We conclude that, for fundamental reasons, the slow time course in our data cannot

![FIG. 15. Predictions for rotation and translation perception from both models. Plots show predictions for 30°/s at 15° tilt. A: predicted angular velocity from the canal–otolith interaction model in combination with leaky integration using original parameters from Merfeld et al. (2005a) (C2, dashed line) and using best-match parameters (C3, solid line). R component of all 6 subjects (thin lines) is also shown. Prediction for angular velocity shows an exponential decay to near zero values, just as in the data. Model C3 performs better than model C2. B: predicted translation velocity from the canal–otolith interaction model with original (C2, dashed line) and adjusted parameters (C3, solid line), superimposed on the T component of all 6 subjects (thin lines). Predicted time course rises faster than the data. C: predicted perceived angular velocity from the frequency-segregation model (F2). Canals and the velocity storage system are modeled by a high-pass filter with a time constant of 23 s. Prediction for angular velocity matches the data quite well. D: predicted translation velocity from the frequency-segregation model with high-pass filter from Telford et al. (1997) and leaky integration (F2) superimposed on the T components of all subjects (thin lines). Discrepancy between the time course of the T component in the data and the model predictions is even larger than that for the canal–otolith-interaction model. Frequency segregation model predicts an immediate onset of translation perception.](http://jn.physiology.org/)

TABLE 5. Performance of two versions of the frequency-segregation model

<table>
<thead>
<tr>
<th>Model</th>
<th>$\tau_{\text{high-pass}}$</th>
<th>$\tau_{\text{leaky}}$</th>
<th>JG</th>
<th>MK</th>
<th>NK</th>
<th>PM</th>
<th>RV</th>
<th>SP</th>
<th>Pooled</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1</td>
<td>0.05</td>
<td>$\approx$</td>
<td>15.8</td>
<td>15.3</td>
<td>13.1</td>
<td>14.4</td>
<td>13.1</td>
<td>11.8</td>
<td>13.9</td>
</tr>
<tr>
<td>F2</td>
<td>0.05</td>
<td>0.68</td>
<td>6.1</td>
<td>3.8</td>
<td>6.9</td>
<td>3.4</td>
<td>6.5</td>
<td>7.2</td>
<td>5.7</td>
</tr>
</tbody>
</table>

Version F1 uses the high-pass filter time constant taken from Telford et al. (1997) and perfect integration. Version F2 uses the same high-pass filter combined with leaky integration. The time constant of the leaky integrator for F2 was determined using pooled data from all conditions and all subjects. Dimensions: $\tau_{\text{high-pass}}, \tau_{\text{leaky}}, \text{RMSE}, \text{deg/s}$. 

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be captured by any of the tested frequency-segregation models. This model version could, however, explain the increase of steady-state velocity with rotation speed. Model F2 actually predicted an increase from about 2.9 to about 6.4 cm/s. The increase with tilt angle was also captured by model F2, which predicts an increase from 4.3 to 8.2 cm/s when the tilt angle increases from 15 to 30°.

In conclusion, we have developed a method to quantify the motion percepts that occur during off-vertical axis rotation. Using this approach, we demonstrated the gradual emergence of an illusory translation percept. Simulations showed that current disambiguation models fail to account for the magnitude of this illusory translation percept, unless the assumption is made that the integration of acceleration signals during OVAR is imperfect. With this allowance and when tuned with an adapted parameter set that differed from the proposal by Merfeld et al. 2005a,b) for self-motion perception in a different stimulation paradigm, the canal–otolith interaction model could approximate the slow time course of the translation percept but not its delay. Despite this restriction, our results clearly suggest a role of canal–otolith interaction in self-motion perception during OVAR. The fact that the model requires different parameter settings for different stimulus conditions points to an additional level of complexity in the system, hitherto not foreseen. The translation results appear to rule out the filter model that matched neither the slow time course nor the delay.

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REFERENCES


